A REVISION OF THE GENERA *NIDALIA* AND *BELLONELLA*, WITH AN EMENDATION OF NOMENCLATURE AND TAXONOMIC DEFINITIONS FOR THE FAMILY NIDALIIDAE (OCTOCORALLIA, ALCYONACEA)

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A REVISION OF THE GENERA *NIDALIA* AND *BELLONELLA*, WITH AN EMENDATION OF NOMENCLATURE AND TAXONOMIC DEFINITIONS FOR THE FAMILY NIDALIIDAE (OCTOCORALLIA, ALCYONACEA)[1]

By HUZIO UTINOMI, D.Sc.

SYNOPSIS

Redescriptions are given of *Nidalia occidentalis* Gray, *Bellonella granulata* Gray and *Bellonella* (*Cereopsis*) *bocagei* (Kent) Wright & Studer, based on types in the collections of the British Museum. A review of all the known species revealed some diagnostic characters and synonymies for the two genera *Nidalia* and *Bellonella*, which are here recognized as valid separate genera belonging to different families.

The family Nidaliidae of Gray is re-established for the generally used name Siphonogorgiidae and the reasons for this are discussed. The unbranched cylindrical Bellonellids, with somewhat contractile calyces, are shown to be essentially primitive, and from them are derived the unbranched Nidaliids and more ramose Siphonogorgiids with firm calyces, though not through the line of Nephtheidae.

The concept now outlined of the supposed evolutionary trends in the Alcyonacea is based mainly on a consideration of the retractility of polyps as a whole and is contrary to earlier ideas of evolution in the group.

I. INTRODUCTION

During the course of working on the octocorallian collections in His Majesty's Biological Laboratory in Tokyo, and, in particular, when reviewing the Japanese species of the so-called genus *Nidalia*, I have come to recognize a distinctive developmental tendency between the species, in spiculation and polyp structure, suggesting a supposed evolutionary trend from the Alcyoniidae to the Siphonogorgiidae. In the meantime, Mr. Frederick M. Bayer of the U.S. National Museum asked me to make a comparison between *Nidalia occidentalis* Gray, type of the genus, and the Indo-Pacific forms of " *Nidalia* ", with a suggestion that the former may be congeneric with a *Cactogorgia*-species from the Indian Ocean, formerly referred to the family Siphonogorgiidae. Subsequently to further this work the authorities of the U.S. National Museum have very kindly presented a topotypic specimen of *Nidalia occidentalis* preserved in that Museum, together with several specimens of some Nephtheid octocorals, to our Laboratory Collection.

[1] Contributions from the Seto Marine Biological Laboratory, No. 307.

The remarkable similarity of the genus *Cactogorgia* to the older genus *Nidalia* led me to re-examine the types of *Nidalia* and *Bellonella*, both of which have been considered synonymous by most of the previous authors. Fortunately I have been able to do this through the generosity of the British Museum (Natural History) and to compare them with the Atlantic and Indo-Pacific (in particular the Japanese) forms. In connexion with this, a more critical review of the allied genera formerly placed in the families Alcyoniidae and Siphonogorgiidae was necessary. In the revision that follows, however, a number of "*Siphonogorgia*" species were either not satisfactorily classified or were left out of consideration, and, in the brief notes below, it has been thought desirable to indicate their present status, and where possible to add new information.

II. REDESCRIPTION OF *NIDALIA OCCIDENTALIS* GRAY

(Text-figs. 1–3)

The following description is mainly based upon a complete specimen presented from the U.S. National Museum and partly (spicules only) upon a fragment of the type material in the British Museum (Nat. Hist.).

MATERIAL EXAMINED. (1) A specimen labelled as "USNM 50398", from *Pelican* St. 169–7: 28° 24·5′ N., 80° 03·0′ W., east of Cape Canaveral, Florida, 45 fms. Jan. 18, 1940.

(2) Two fragments from the holotype in the British Museum, from off Montserrat, West Indies; depth unknown.

DESCRIPTION. The colony from east of Cape Canaveral, Florida, is attached to a sedentary polychaete tube, on which a young colony of a Muriceid gorgonid, *Thesea grandiflora*, was also living. It is torch-like in form, consisting of a barren rigid stalk tapering downwards, and an expanded head-like polyparium covered with a number of large verrucae (more than 40) close together at the slightly convex summit. The total height is 22 mm., of which about 17 mm. belongs to the stalk proper; the polyparium is 9 mm. in diameter and about 5 mm. high in the middle. The largest verruca at the summit of polyparium is about 1·5 mm. in diameter and about 0·88 mm. in height, and as its tip is blunt, the margin appears rounded.

The anthocodiae are completely withdrawn into the verrucae. They show a well-developed armature at their head. It consists of the eight points and a number of collaret rows transversely arranged below, both of which show considerable irregularity in the size and arrangement of spicules. In more regular arrangement the anthocodial spicules may be counted about 4–5 pairs *en chevron* in each point and up to about 15 transverse rows in the collaret.

The tentacles, which are simply infolded over the mouth in the contracted condition, are probably up to 2 mm. in length when fully exserted and bear about 7–8 pairs of long pinnules. Their aboral surface is densely packed with small, slightly roughened, rodlets which tend to be arranged *en chevron* and become larger towards the base, whereas the pinnules are apparently devoid of spicules or have a few very minute rodlets.

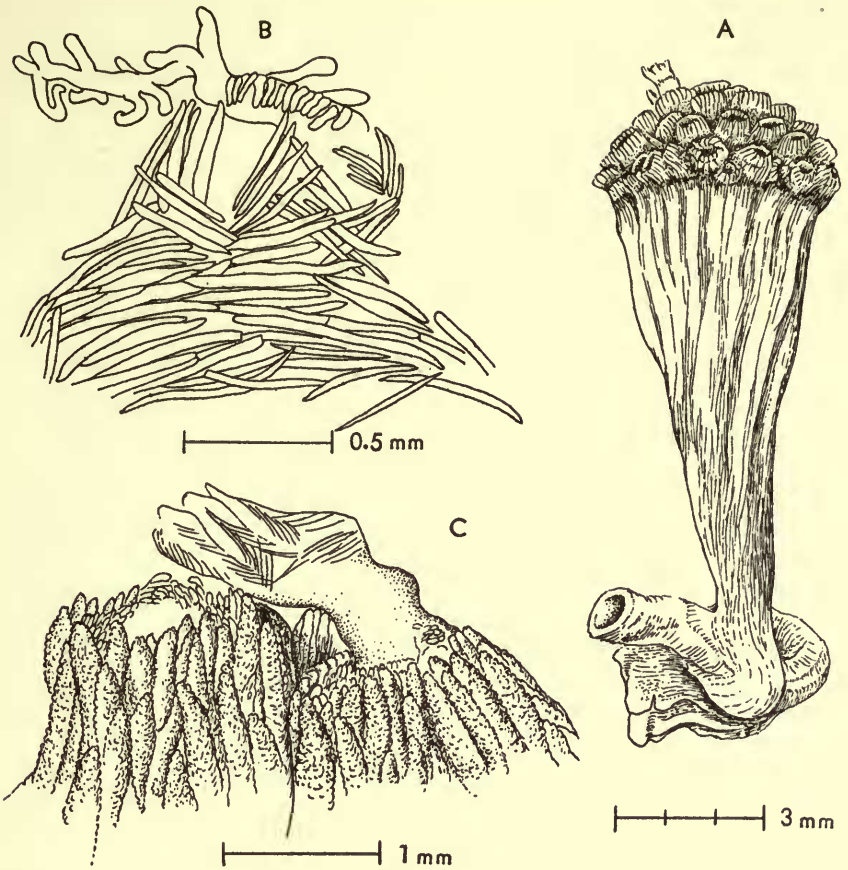

FIG. 1. *Nidalia occidentalis* Gray: A, a specimen from East of Cape Canaveral, Florida, 45 fms.; B, anthocodial spiculation in two points and in a tentacle; C, tip of two verrucae, with a polyp extended. Note a number of minute scale-like sclerites inside the tip of verrucae.

The middle part of the introvertible neck zone (" the introvert " of Deichmann) is wholly bare just below the collarets, while at its base, lining the tip of the verrucae, there are numerous very small, colourless, oval scales which are irregularly set, but roughly arranged in the eight interseptal tracts.

The verrucae, i.e., the unretracted thickened part of the polyps, are supported by very firm walls densely packed with large stout spindles similar to those of the stalk. These spicules are longitudinally disposed close together, and are not grouped in eight regions.

The stalk is deeply furrowed longitudinally on the surface due to the longitudinal arrangement of large spicules, which are all strongly tuberculated spindles up to 2·5 mm. in length, covered with compound tubercles, simply or in clusters. The coenenchyme is also densely spiculose, since the canal-walls are very compact with

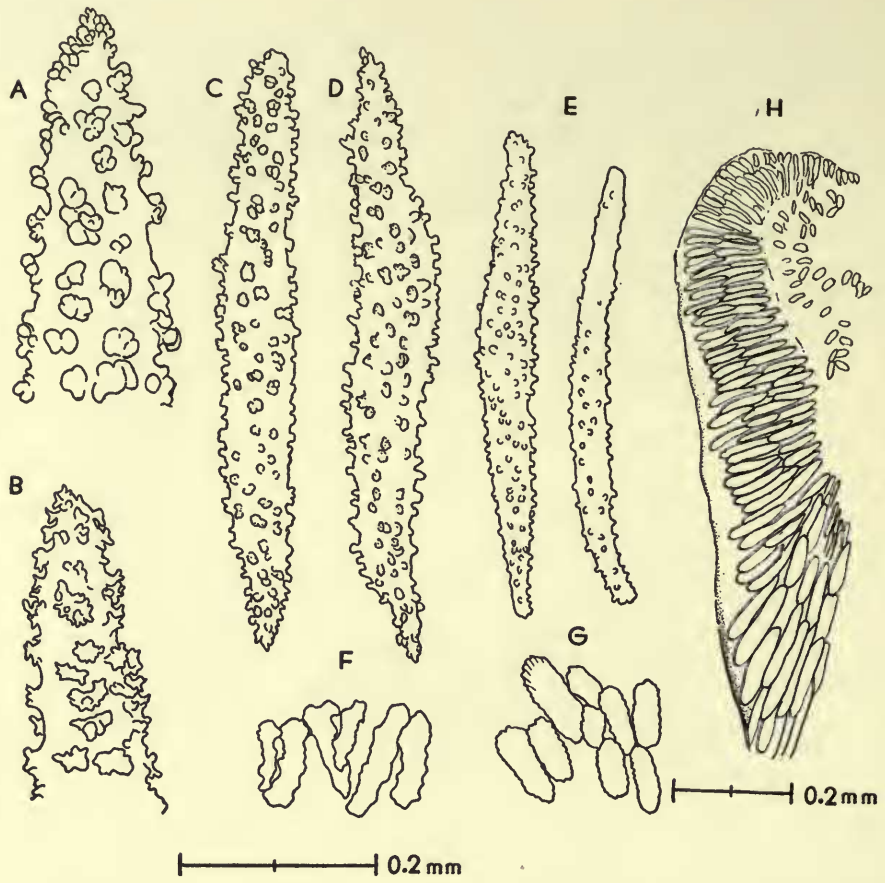

FIG. 2. *Nidalia occidentalis* Gray : A and B, part of larger spicules from stalk rind ; C, typical spindle of stalk rind ; D, typical spindle of verrucae ; E, anthocodial spiculae ; F, flat rodlets from tentacle ; G, scales from introvert ; H, side view of tentacle with dense arrangement of spicules (from the type specimen of Gray). Scale on the left applies to A–G, and that on the right to H only.

similar spindles longitudinally disposed, without any sign of the boundary or the difference in size and shape of spicules separating the interior from the surface layer.

The colour of the specimen is orange-yellow in alcohol, paler towards the base of the stalk, due to the degree of preservation of the colour of spicules themselves. The anthocodial spicules, together with those of introverts are, however, colourless.

Measurements of Spicules (in mm.).

Anthocodial spicules :

Point—warty spindles with simple warts. 0·36 × 0·035 ; 0·4 × 0·035.

Collaret—do. 0·4 × 0·05 ; 0·56 × 0·05 ; 0·6 × 0·035.

Tentacle—flat rodlets with jagged furniture. 0·1 × 0·036 ; 0·12 × 0·03 ; 0·14 × 0·028.

Introvert—scales with scalloped edges. 0·06 × 0·028 ; 0·075 × 0·028 ; 0·09 × 0·036.

Stalk spicules :

Verruca—multituberculate spindles. 1·0 × 0·23 ; 1·2 × 0·17 ; 1·5 × 0·3.

Stalk (incl. surface and interior)—do. 1·4 × 0·17 ; 1·5 × 0·29 ; 2·0 × 0·32.

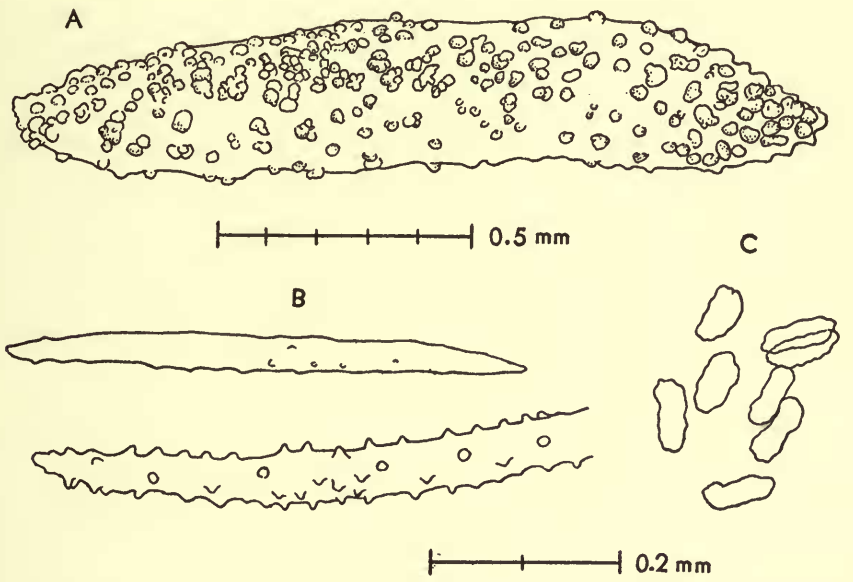

FIG. 3. *Nidalia occidentalis* Gray : A, spindle from stalk rind ; B, anthocodial spindles ; C, scales from introvert. All spicules from the type specimen in the British Museum (Nat. Hist.).

REMARKS. This specimen as described above corresponds exactly with the type of Gray in details of the structure and spiculation ; some spicules of the latter are shown in text-fig. 3 for comparison. Deichmann (1936, p. 56) described an additional species, *Nidalia rigida*, but the two are so alike that it is not possible to separate them from each other specifically.

Cactogorgia simpsoni (taken at " Siboga " St. 289) which was fully described and figured by Thomson & Dean (1931, p. 184) is, curiously enough, in general agreement with this *Nidalia occidentalis*, in spite of the considerable distance separating their localities.

In particular, the occurrence of numerous small oval scale-like sclerites in the neck zone or " introvert ", a character which had not been noted in the remaining species of *Cactogorgia*, proves the former to be identical with the latter. It is indeed wonderful that only Mr. Frederick M. Bayer (personal communication) seems to have noticed this similarity.

TYPE LOCALITY. Off Montserrat, West Indies.

DISTRIBUTION. Atlantic coast of North America and West Indies from off South Carolina to off Barbados, in 38–170 fms. (Deichmann, 1936 ; Bayer, 1952 ; 1954*a* ; as *Nidalia occidentalis*) ; off Timor, Arafura Sea, 112 m. (Thomson & Dean, 1931, as *Cactogorgia simpsoni*).

III. REDESCRIPTION OF *BELLONELLA GRANULATA* GRAY

(Text-fig. 4)

Bellonella granulata Gray, the type species of *Bellonella*, was only briefly described from Bellona Reef, north-west coast of Australia, with only a figure of the total animal (Gray, 1862 ; p. 35). Since then, it has not been found again except for an enigmatic record by Thomson & Dean (1931) from " Siboga " St. 240, in the Banda Sea, at a depth of 9–45 m., which is only a moderate distance from the type locality.

As regards the spiculation, Gray mentions only that " It has some characters in common with my genus *Nidalia* but differs from it in the surface of the coral being minutely granular, and not spiculose." This very brief account led all later students, especially Kükenthal, to misinterpret the status of the genus in the classification of this group. Therefore, the re-examination and fuller description of Gray's type specimen seemed highly desirable, and this was now made possible through the re-examination of material from the British Museum.

MATERIAL EXAMINED. Spicules of type material on two mounted slides.

DESCRIPTION. The type specimen itself could not be examined by me, but, as inferred from the original figure given by Gray (1862, p. 34), the colony consists of a cylindrical stalk somewhat expanded at base and a capitate polyparium. A number of polyps, crowded together at the top of hemispherical head, apparantly resembling those in the preceding *Nidalia occidentalis*, are completely retractile, and when at rest their verrucae appear 8-lobed at the tip as in most of the other *Bellonella* species, and not truncated.

The outer surface of the stalk without polyps is minutely granular according to Gray. This granular appearance depends upon the dense covering of minute spicules, some of which are figured here for the first time. The spicules are slender thorny spindles, or clubs with more spiny heads derived from spindles. The spindles are usually longer than the clubs, and they are all transparent and colourless, though some retain still a slightly rosy hue around the axis (see Text-fig. 4B).

According to Gray, " the base of the polyps is strengthened with very minute spicula, placed in a longitudinal series parallel to each other." These spicules are also transparent, slightly rosy to yellowish in colour and somewhat club-like in form, bluntly headed (see Text-fig. 4A).

Measurement of Spicules (in mm.).

Stalk spicules :

Spindles—0·17 × 0·04 ; 0·25 × 0·07 ; 0·28 × 0·05 ; 0·32 × 0·035.

Clubs—0·1 × 0·05 ; 0·14 × 0·05 ; 0·17 × 0·05 ; 0·25 × 0·05.

Polyp spicules :

Clubs—0·16 × 0·035 ; 0·19 × 0·05 ; 0·25 × 0·05 ; 0·28 × 0·05.

REMARKS. According to Thomson & Dean (1931), a small specimen, taken at

" Siboga " St. 240, which was recorded under the name " *Nidalia granulata* (Gray) " is about 1·5 cm. in height, with a maximum diameter of 5 mm. and ochraceous in colour. The coenenchymal spicules are said to be " minute double spheres, knobbed capstans, a few warty rods " and practically no spindles are included. It is thus beyond doubt that they have erroneously identified this specimen, without making reference to the type specimen. Their description without figures is too inadequate to permit any other suggestions.

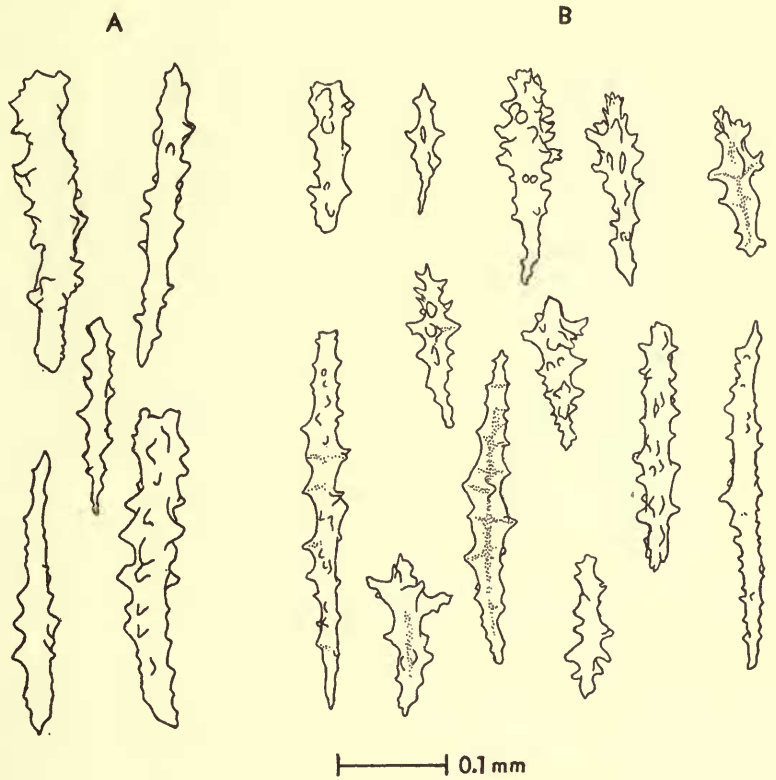

FIG. 4. *Bellonella granulata* Gray : A, spicules from the polyps ; B, spicules from the stalk. All spicules from the type specimen in the British Museum (Nat. Hist.).

DISTRIBUTION. Type locality only—Bellona Reef, north-western coast of Australia, 17 fms.

IV. REDESCRIPTION OF *BELLONELLA BOCAGEI* WRIGHT & STUDER

(Text-figs. 5–6)

The following description is based on fragments of the material of *Bellonella bocagei* (Kent), collected by the *Challenger* from the west of Azores, and now in the collections of the British Museum.

DESCRIPTION. The specimen is excellently figured by Wright & Studer (1889, p. 241 ; pl. 37, fig. 2) as here reproduced in text-fig. 5A, but their description is not sufficiently detailed for recognition of the species.

The specimen figured forms a cylindrical colony arising from a flat extended base. As measured from the original figure, it rises from the base to a height of about 6 cm., with a diameter of about 8 mm. in the middle of the stalk. The upper half is rather loosely covered with large cylindrical polyps, and the lower half is apparently bare, bearing no polyps at all.

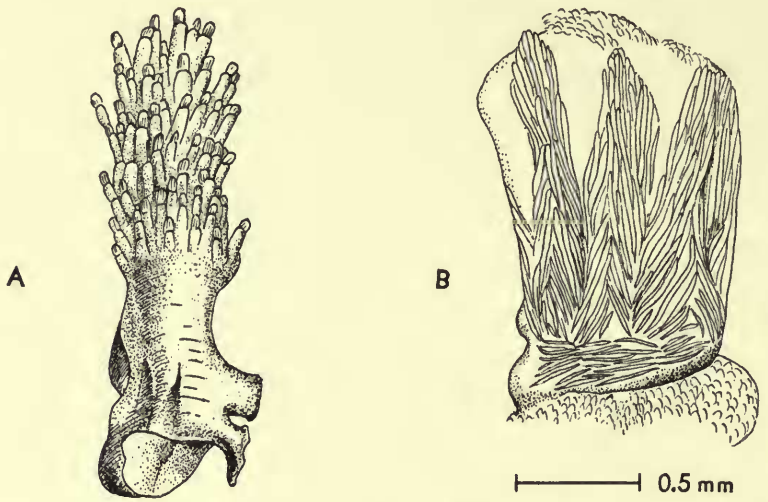

FIG. 5. *Bellonella bocagei* (Kent) : A, a *Challenger* specimen (redrawn from Wright & Studer, 1889) ; B, anthocodia with partially contracted anthostele.

When extended, the polyps may attain a length of about 2 mm., with a diameter of about 0·8 mm. at the head. At the base each forms an 8-lobed, low verruca which is thick-walled and spiculiferous. The tentacles bear slender, curved or spiny, flat rodlets on the aboral side. The anthocodial armature consists of 8 double rows of steeply-converging slender spindles with low warts and bluntly ended. Below these the similar spindles are arranged in about 10 transverse rows, and they become sparser and smaller in size in the eight interseptal tracts of the neck zone down to the basal calyx (Text-fig. 5B).

The stalk cortex is closely packed with long, spiny spindles or shorter, spiny clubs thickened at upper end. The coenenchyme contains more slender spindles with high warts.

All these spicules are usually transparent and colourless, but some reddish ones are found on the cortex of polyparium.

Measurements of Spicules (in mm.).

Anthocodia—0·25 × 0·05 ; 0·35 × 0·05 (Text-fig. 6A).

Tentacle—0·09 ~ 0·14 × 0·01 ~ 0·02 (Text-fig. 6B).

Neck zone—0·035 ~ 0·055 × 0·01 ~ 0·03 (Text-fig. 6C).

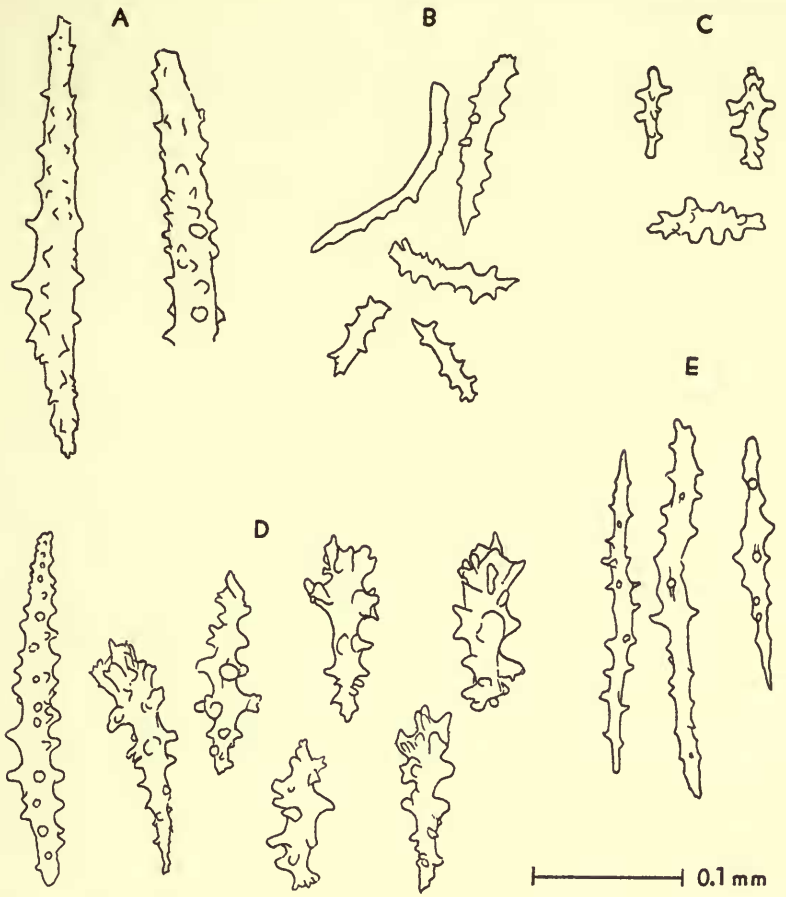

FIG. 6. *Bellonella bocagei* (Kent) : A, anthocodial point spicules ; B, tentacle spicules ; C, spicules from neck zone ; D, spicules from stalk rind ; E, coenenchymal spicules in canal-walls, All are drawn from a specimen in the British Museum (Nat. Hist.).

Stalk cortex—0·09 × 0·035 ; 0·12 × 0·05 ; 0·23 × 0·035 (Text-fig. 6D).

Coenenchyme—0·09 ~ 0·25 × 0·009 ~ 0·017 (Text-fig. 6E).

REMARKS. This species was originally described by W. Saville Kent (1870, p. 398) under the name *Cereopsis Bocagei* gen. nov. et sp. nov., from specimens taken off Setubal, Portugal in 15 fms. Wright & Studer (1889) identified this specimen with Kent's species and transferred it to Gray's genus *Bellonella*, together with *Nidalia atlantica* Studer (1878, p. 635) and *Itephitrus*[1] *speciosus* W. Koch (1886) recorded from the neighbouring waters as synonyms. This procedure was followed by Pütter (1900) who reviewed the hitherto known species of *Bellonella*. Most of the later authors, however, regarded this species as a member of *Gersemia* (Kükenthal,

[1] Erroneously called *Iphethyrus* or *Iphythyrus* by Wright & Studer and May respectively.

1906*a*, *b*, 1907; Thomson, 1927) or as a member of *Alcyonium* (Molander, 1915; Deichmann, 1936).

Apart from a problem concerning the distinction between the families Alcyoniidae and Nephtheidae from which such different opinions were probably derived, I came to the conclusion, by a close comparison of all Japanese species of *Bellonella* with other related genera of both families, that its assignment to the genus *Bellonella* is highly advisable as proposed by Wright & Studer.

DISTRIBUTION. Off Setubal, Portugal, 15 fms. (Type locality); off Senegal, tropical West Africa, 115 fms. (" Gazelle " St.); west of the Azores, 450 fms. *Challenger* St.; Rolas, Gulf of Guinea; Azores, 845 m.[1] (" Prince Albert I " St. 584).

V. VALIDITY OF THE GENUS *BELLONELLA* AND ITS SYNONYMY

As mentioned above, the genus *Bellonella* was created by Gray (1862) for a single species *B. granulata*, and later (1869) placed in his family Bellonelladae near the Xeniidae. At that time he recognized an obvious difference in spiculation separating it from his earlier genus *Nidalia* although he did not go into details.

His systematization of various octocorallian genera has not, in general, been accepted in modern systems of classification, and his views on the distinguishing characters between *Bellonella* and *Nidalia* have been opposed by most later authors. Wright & Studer (1889) at first suggested the probable identity of both the genera, though actually treating them separately. In recent years the two genera have been united by May (1900), and in particular, by Kükenthal (1906*a*, *b*), who was convinced that some species contained in the genus *Bellonella* (*Nidalia* in his sense) should be retained in the Alcyoniidae, while others like *Gersemia* and *Capnella* should be transferred to the Nephtheidae.

Among recent authors, only J. S. Thomson (1910, 1921) expressed a doubt as to whether Gray's *Nidalia* and *Bellonella* are really identical, and referred two South African species to the latter genus as *B. studeri* n. sp. and *B. rubra* Brundin. In addition to these, he recognized Pfeffer's *Metalcyonium* as a distinct genus from *Bellonella*, referring three species to it.

Prior to him, Kükenthal (1906*a*) divided the genus *Alcyonium* Linnaeus into three subgenera, *Alcyonium* s. str., *Metalcyonium* and *Erythropodium* (later changed as *Parerythropodium*). Although this attempt has not been followed by most other authors, especially Molander (1915), it is undoubted that *Metalcyonium* is a unique group embracing the species which are clavate, capitate or mushroom-shaped and ordinarily unbranched in form. Most of them were known from the subantarctic region (Patagonia and South Africa), but later a few were recorded from Amboina, East Indies (Burchardt, 1902) and northern Japan (Yamada, 1950).

Judging from the descriptions given by Pfeffer (1889) and Kükenthal (1906*a*), and also from photographs published by Molander (1929, pl. IV, fig. 9), *Metalcyonium clavatum* Pfeffer, which is the type of the genus, seems to be very different from others since referred to the genus (or subgenus) in its form of growth. Although I

[1] Thomson's identification is still in doubt (*see* Deichmann, 1936; p. 51).

have no personal knowledge of this species, its close affinity with the genus *Bellonella* cannot be denied.

Kükenthal (1906*a*, *b*), in dividing the family into two subfamilies, Nidalliinae (*sensu* Kükenthal) and Alcyoniinae, emphasized that the canal system is direct and partly indirect in the former, while indirect in the latter. Such a difference was, however, strongly rejected by Molander (1915).

According to Molander, *Metalcyonium clavatum* often shows a sign of slight division of the polyparium into side branches (or lobes). Here I only wish to point out that on investigating the Japanese species of *Bellonella* such examples as *M. clavatum* could be observed normally or abnormally (Utinomi, 1957).

Even if this *M. clavatum* can be regarded as belonging to *Bellonella* on account of the unbranched cylindrical form of growth, this cannot be applied to other mushroom-like forms such as *M. capitatum* Pfeffer, *patagonicum* May, *molle* Burchardt and *novare* Kükenthal, as well as other unbranched alcyoniids tentatively referred to the genus *Alcyonium* in the widest sense (for example, see J. S. Thomson, 1910 ; Yamada, 1950 and Tixier-Durivault, 1954).

If this re-grouping is actually justified as limited by the type designation for Pfeffer's genus *Metalcyonium*, these capitate forms are left without a genus and therefore require a new genus or subgenus name. But for the present, the differences between these unbranched, either cylindrical or capitate, forms of *Metalcyonium* and many of lobate or branched forms of the true *Alcyonium* s. str. are so vague, that only by a complete revision can their status be decided.

In this revision below, though admittedly not complete, the position of the species which have been referred to *Nidalia* (*Bellonella*) or other genera is considered chronologically and the conclusion reached earlier for others are re-stated briefly.

Bellonella granulata Gray (1862) is designated by monotypy as the type of a valid genus *Bellonella* Gray, 1862.

Cereopsis Bocagei Kent (1870) is, as mentioned above, referable to *Bellonella*, following Wright & Studer (1889) and May (1900). Its assignment to either *Alcyonium* or a Nephtheid genus *Gersemia*, as proposed by later authors, is not adequate.

Another species *C. studeri*, described by von Koch (1891) from Naples, Italy, was referred to *Nidalia* by May, and then to *Gersemia* by Kükenthal. This species was later re-discovered and fully described by Thomson & Dean (1931) from the East Indies and by Stiasny (1941) from Naples, under the original name. Very recently I had a similar specimen, referable to this species, from Sagami Bay, Japan (unpublished) and noted some remarkable characters generically distinguishable from the type species of *Cereopsis*. Therefore, the genus name *Cereopsis* cannot be used for both *bocagei* and *studeri* as a synonym of *Bellonella*, though it was later replaced by the substitute name *Cereopsida* Strand (1928). Koch's *studeri* appears to be generically distinct from the type species *bocagei*, and therefore requires a new genus, for which the new name **Kochella** is here proposed. Detailed discussion as to this form will appear in another paper.

Nidalia atlantica Studer (1878, p. 635)

Itephitrus speciosus W. Koch (1886, p. 1)

Both species are probably synonymous with *Bellonella bocagei* (Kent), together with the *Challenger* specimen described above.

Nidalia arctica Danielssen (1887, p. 119)

This species, together with *Organidus nordenskjöldi* and *Krystallofanes polaris* succeedingly described in the same paper, are probably not Bellonellids but may be merely young or stunted specimens of *Gersemia fruticosa* (Sars) (= *G. rubiformis, sensu* Madsen, 1944).

Bellonella variabilis Studer (1901, p. 25)

(= *Rhodophytum variabile* Studer, 1890, p. 89)

Kükenthal (1906*a*, *b*) referred this species to *Gersemia*, but Molander (1915) who studied Studer's original type, and Deichmann (1936) consider it a stunted specimen of *Alcyonium glomeratum* Hassall with the least development of polypiferous lobes.

Bellonella rubra Brundin (1896, p. 6)

Bellonella cinerea Brundin (1896, p. 8)

Both species first recorded from Japanese waters distinctly belong to *Bellonella*. The identity of the latter with the former, as proposed by Kükenthal, is still open to question and must await the discovery of more material.

Bellonella rigida Pütter (1900, p. 448)

Eleutherobia japonica Pütter (1900, p. 449)

The latter is undoubtedly a synonym of the former. This is a sand-dwelling form, where the stalk is often rounded at the base, apparently as in the pennatulids, such as *Cavernularia* and *Veretillum*. In fact, Thomson & Rennet (1927, p. 143) carelessly included it in the report on the Japanese species of pennatulids.

Nidalia foliacea May (1900, p. 101)

Probably identical with a Nephtheid *Capnella imbricata* (Quoy & Gaimard).

Bellonella indica Thomson & Henderson (1905, p. 274)

Probably a valid species with coenenchymal spicules of capstan type.

Bellonella studeri J. S. Thomson (1910, p. 550)

Bellonella rubra Brundin (J. S. Thomson, 1910, p. 554)

Metalcyonium clavatum Pfeffer (J. S. Thomson, 1910, p. 556)

These three species recorded from South Africa are probably valid species of *Bellonella*. But the second species may be different from the species occurring in Japan. According to Molander (1929), the third is not the same as the typical species from South Georgia.

Nidalia rubra (Brundin) (Tixier-Durivault, 1954 ; p. 127)

Nidalia morifera Tixier-Durivault (1954, p. 128)

The former, though briefly described, may be similar to the species of the same name from South Africa, which is mentioned above. The latter is a peculiar *Bellonella*, closely resembling *B. grayi* (Thomson & Dean, 1931) in having an indistinct sterile stalk and in having no spicules in the anthocodiae.

Apart from these, a number of new species have been described by Kükenthal (1906*b*), Nutting (1912) and Thomson & Dean (1931), all referring to *Nidalia*. The majority of them should be placed in the genus *Bellonella* as valid species, but only a direct comparison with their types will decide it. Further information as to the synonymies and affinities is given in my recent paper reviewing Japanese species of *Bellonella* (Utinomi, 1957).

Consequent upon re-examination of the types of both *Nidalia* and *Bellonella* and

a review of all previous records referred to both genera and related genera, a revised diagnosis of the genus *Bellonella* Gray is given below :

Diagnosis. Alcyoniids whose colonies are cylindrical or subcylindrical. Colony with a stalk and an unbranched (scarcely slightly-lobed) cylindrical polyparium. Polyps large, monomorphic, fully-retractile within 8-lobed, or truncated, calyces. Gastric cavities of all polyps closely fascicled, extending to base. Anthocodiae, with or without, 8-chevroned rows of spicules. Coenenchymal spiculation sparse but dense in outer cortical layer. Spicules : spindles, rods, clubs and capstans. Usually vividly coloured. Living in deep waters of all the oceans.

Type species : *Bellonella granulata* Gray (1862).

VI. SYSTEMATIC POSITION OF THE GENUS *NIDALIA* AND ITS RELATIONSHIP WITH SIPHONOGORGIIDS

The genus *Nidalia* was erected by Gray (1835) to contain a single species, *N. occidentalis*, from off Montserrat, West Indies. The original description given by Gray is quite insufficient for the diagnosis of the genus and species, and there was no figure or description of the spicules. Accordingly, regrettably enough, Studer (1901) and Kükenthal (1906*a*, *b*) merged the genera *Nidalia* and *Bellonella* as synonymous. The former authority used the name *Bellonella*, while the latter on the contrary the older name *Nidalia* as the generic name. Nevertheless, Kükenthal actually neglected to consider the name of *Nidalia occidentalis*, which is the type species, in recording all of the hitherto known and undescribed species of the genus (*Nidalia* or *Bellonella*). It is possible that he might have denied its actual existence. This confusion might be due to the lack of exact knowledge of both the types, and the superficial resemblances of the colonies, based mainly on the imperfect descriptions of Gray.

Since the original descriptions, both the type species were not found again for many years. Deichmann (1936) was apparently the first to recognize *Nidalia occidentalis* as a distinct species and genus. At the same time she described another species (*N. rigida*), but her species cannot be regarded as distinct and she did not put forward any further comparison with the Indo-Pacific forms of " *Nidalia* ". Accordingly, more recent workers, including myself, have followed Kükenthal in considering *Bellonella* a synonym of *Nidalia*.

As has already been remarked in the preceding chapters, *Nidalia occidentalis* Gray differs considerably from *Bellonella granulata* Gray and the allied forms. The differences justify separating the two as different genera and even different families, the former as a member of " Siphonogorgiidae ", and the latter to the Alcyoniidae.

The diagnostic salient characteristics of *Nidalia occidentalis* may be summarized below :

The colony is torch-like (instead of cylindrical in a strict sense), unbranched, with an expanded hemispherical capitulum covered with large crater-like calyces. Calyces are not 8-lobed, but are truncated at the tip, and thick-walled, being closely packed with large, multituberculate spindles arranged longitudinally. Coenenchymal spiculation in the stalk is more rigid, giving the whole colony a brittle consistency.

These characters indicate its closest affinity with the " Siphonogorgiidae " amongst families of the Alcyonacea.

In searching in literature I have not seen it mentioned in any paper, where it might be expected to be found. As mentioned above, only Mr. Frederick M. Bayer (personal communication) seems to have been aware of a remarkable similarity between *Nidalia occidentalis* and *Cactogorgia simpsoni*.

The genus *Cactogorgia* was established by Simpson (1907 ; see also, Thomson & Simpson 1909, pp. 143–150) for three species, showing different growth forms, collected by the R. I. M. S. ship *Investigator* in the Indian Ocean. They are *C. celosioides* from Andamans (depth unknown), *C. expansa* from off Cape Comorin in 38 fms. and *C. alciformis* from Andamans and off Arakan coast from 13 fms. Since then, three more species have been recorded, also from the Indian Ocean. They are *C. lampas* Thomson & Mackinnon (1910) from the Seychelles from 37 fms., *C. agariciformis* Simpson (1910) from an unknown locality and *C. simpsoni* Thomson & Dean 1931) from " Siboga " St. 289 (9° 0·3′ S., 126° 24·5′ E., 112 m., SE. of Timor).

Notwithstanding the differences in the shape of the colony and the anthocodial armature, all of these species agree well with one another in not having any definite branching and in having a marked distinction into sterile trunk and polyp-bearing portion, and in showing dense spiculation of the canal-walls, as well as in the rind. In addition, all spicules are very large, stout, highly-tuberculate spindles of the *Siphonogorgia*-type, and the tentacle spicules are minute, scale-like ; the anthocodiae show the definite " crown and points " armature arrangement and are completely retractile within the thick-walled verrucae, as in *Nidalia occidentalis* and many of *Siphonogorgia* species. They are generally yellow to orange coloured. Therefore I do not hesitate to regard the two genera as congeneric, and in doing so note that *Nidalia* has priority over *Cactogorgia* as the generic name.

As regards the systematic position of this *Cactogorgia* and also *Agaricoides* (Simpson, 1905 ; Thomson & Henderson, 1906), opinions differ between the British and German authorities. Originally Simpson placed both among the Siphonogorgiinae (as a subfamily of the Nephtheidae) on account of the rigid consistency of the colony caused by the dense spiculation in the coenenchyme. Among recent authors, for example, Chalmers (1929), Hickson (1930) and Bayer (1956) consider that they are more closely related to the family Siphonogorgiidae than to any other.

Kükenthal (1896) raised the subfamily Siphonogorgiinae to the rank of a separate family as Siphonogorgiidae in the belief that *Siphonogorgia* is intermediate in form between the Nephthyidae (= Nephtheidae) and the Gorgoniidae (= Gorgonacea, in particular, Scleraxonia). Nevertheless, later (1906*b*, 1910) he pointed out the dissimilarity of Simpson's two new genera to the gorgonids, suggesting only a near relationship of *Agaricoides* to *Nidalia* (= *Bellonella*) *macrospina* Kük. and that of *Cactogorgia* to *Nidaliopsis pygmaea* Kük., both belonging to the Alcyoniidae.

From an examination of *N. macrospina* from Japan Kükenthal's suggestion is amply confirmed. In this connexion, a note by Thomson & Simpson (1909, p. 135) recalls that *Siphonogorgia annectens* n. sp. " bears a strong resemblance to *Nidalia macrospina* Kükenthal." This siphonogorgiid is, according to Macfadyen (1936), probably synonymous with *Nephthyigorgia pinnata* which genus was created by Kükenthal (1910) for three Australian species showing a poor internal spiculation in the stem. This view also may possibly be right.

If these closer relationships to either of the two families Siphonogorgiidae and

Alcyoniidae (instead of Nephtheidae as generally accepted) are actually justified, then we are faced with the alternatives of expanding the definition of either of the two families generally accepted or erecting a new separate family for these unbranched forms.

A search of the literature on *Siphonogorgia* Kölliker (including *Chironephthya* Wright & Studer), comprising a large number of species, reveals that the hardness of coenenchymes due to the dense internal spiculation, given by Wright & Studer (1889) as diagnostic, is quite untenable. As can be deduced from a list of hitherto known species of *Siphonogorgia* given by Thomson & Dean (1931, pp. 153–166), the coenenchymal spiculation especially in the canal-walls is very variable, and in another closely related genus, *Nephthyigorgia*, the distribution of spicules is largely confined to the outer layer (usually called cortex or rind).

The rigid consistency and brittleness of the colony which characterize *Siphonogorgia* and allied genera are mainly due to the thick wall formed by a definite close arrangement of longitudinally-disposed, large spindles, regardless of internal spiculation whatever. Therefore, the colonies are decidedly different structurally from those of the Gorgonacea, since no spicular axis as seen in the Scleraxonian gorgonids is formed in the interior, although there may be a superficial resemblance in the mode of growth.

In both the genera mentioned above, *Nidalia* (*Cactogorgia*) and *Agaricoides*, the colonies are generally unbranched, like alcyoniids such as *Bellonella* and *Anthomastus*, but the spiculation of the cortex and the structure of polyps are more closely related to the Siphonogorgiidae than to the Alcyoniidae. Thus it seems better to include both under the former group as a special subfamily rather than to erect a separate family.

In doing so, however, the generally used family name Siphonogorgiidae (*pro* Siphonogorgiaceae Kölliker, 1875, p. 22) should be displaced by the name Nidaliidae (*pro* Nidalidae Gray, 1869, p. 127), since the latter has priority over the former as the family name. Gray's diagnosis, that is " Coral simple or branched ; stem cylindrical, cartilaginous, with a crustaceous skin and imbedded spicules. Polypes on the upper surface of a hemispherical head, with prominent large conical polype-cells ; stem and polype-cells covered with fusiform spicules " is applicable to this family without much alteration of diagnostic characters.

Below I propose a new system of classification based on the revised examination of the type specimen of *Nidalia* and reconsideration of the diagnostic characters of the allied genera, formerly assigned to the Siphonogorgiidae, in recognition of the distinctive evolutionary trends they display.

Family Nidaliidae Gray, 1869

Nidalidae Gray, 1869, p. 127.

Siphonogorgiaceae Kölliker, 1875, p. 22 ; Klunzinger, 1877, p. 48 (as subfamily of Alcyonidae in Alcyonacea).

Siphonogorginae Wright & Studer, 1889, p. 226 ; Thomson & Henderson, 1906, p. 11 ; Thomson & Simpson, 1909, p. 124 (as subfamily of Nephthyidae).

Siphonogorgiidae Kükenthal, 1896, p. 133 ; May, 1900, p. 171.

Siphonogorginae (*sic*) Hickson, 1903, p. 487 (ranked however as a family).

Siphonogorgiidae Kükenthal, 1906*b*, p. 68 ; Harrison, 1909, p. 31 ; Hickson, 1930, p. 244 ; Thomson & Dean, 1931, p. 149 (part) ; Bayer, 1956, p. 188 (part).
Not Nidaliinae Kükenthal, 1906*a*, p. 29 (as subfamily of Alcyoniidae).
Not Nidalinae (*sic*) Kükenthal, 1906*b*, p. 19 (as subfamily of Alcyonidae).

Emended Diagnosis. Colonies unbranched or tree-like, branched with stiff, cylindrical branches. Outer surface very roughened, closely-packed with large, multi-tuberculate spicules longitudinally-disposed, which give the colony a rigid brittle consistency. Anthocodiae completely or partially retractile, within densely spiculose tubulo-conic verrucae, more or less projecting above the surface. Anthocodial armature with symmetrical " points and crown " arrangement.

Subfamily Nidaliinae nov.

Unbranched, or slightly branched only at base ; colonies with a marked distinction into trunk and polyp-bearing portion ; densely spiculose throughout ; polyps completely retractile.

For the present, only two genera *Nidalia* Gray (= *Cactogorgia* Simpson) and *Agaricoides* Simpson are known as belonging to this subfamily.

Subfamily Siphonogorgiinae Kölliker

Profusely or feebly branched, tree-like colonies not distinctly separable into trunk and polyp-bearing branches ; canal-walls filled, densely or loosely, with spicules similar to those of rind ; polyps singly or closely-arranged on stem and completely or partially retractile.

Siphonogorgia Kölliker is a representative genus among this group. *Nephthyigorgia* Kükenthal is also probably distinct, but *Dactylonephthya* Thomson & Simpson seems unique in the absence of distinction between the anthocodiae and verrucae, if this proves to be correct. Here it is tentatively placed near the position of *Siphonogorgia*, but its re-discovery is much needed.

The remaining genera, such as *Scleronephthya* Wright & Studer and *Stereacanthia* Thomson & Henderson, if distinct as genera, may be grouped within the Nephtheidae, together with *Capnella* (= *Paranephthya*) and *Lemnalia*.

VII. Evolutionary Interrelationship between Alcyoniidae and Nidaliidae (Siphonogorgiidae auct.)

Our knowledge of the interrelationships of various groups and their evolutionary trends in the Alcyonaria is very incomplete. Kükenthal (1906*a*) has discussed the evolution of the Alcyonacea, concluding that the Siphonogorgiidae are the most evolved group derived from a supposed solitary *Haimeia*-like ancestor along a line Cornulariidae-Xeniidae-Alcyoniidae-Nephtheidae. But this monophyletic view has not been supported by later workers (in particular, Molander, 1915). Within the Alcyoniidae, Molander supposed two different lines of evolution as regards polyp dimorphism (one includes the monomorphic forms, and the other, the dimorphic

forms) and thought that *Nidalia* (*sensu* Kükenthal) was the most primitive genus. His view seems to me adequate, but he did not extend his views to mention any further evolutionary lines along which they may have evolved.

As discussed above, *Bellonella* (namely, *Nidalia sensu* Kükenthal) is more primitive than the lobated or ramified forms of *Alcyonium* for reasons already given, and it is among this genus that we have to look for forms resembling the ancestral retractiel stoloniferans. *Nidalia* (*sensu* Gray), on the contrary, is a more advanced or specialized form to be placed near *Siphonogorgia*, although it is ordinarily unbranched in its mode of growth.

The two genera have been treated as synonymous for many years, perhaps because of the lack of true knowledge of the original types of the two, or of confusion with regard to the species status due to the superficial resemblance of the colonies.

The most primitive forms, such as *B. rubra* and *B. grandiflora*, retain the flaccid consistency of the coenenchyme, of which canal-walls are thick but not so densely spicular as in the rind. The coenenchymal spicules are of uniform shape and small in size, and the anthocodial armature retains many ancestral features seen in stoloniferans. The retractile polyp is very large, supported by a long stalk with flexible armature of small spicules continued downwards as 8 interseptal areas, so that, in contraction the short stiffened lower part of the polyp itself, called anthostele, is infolded to cover over the retracted anthocodia, forming a 8-lobed wart-like operculum by which the mouth is completely closed.

In these species showing the 8-lobed anthostele (" calyx "), the arrangement of spicules on the surface is ordinarily continuous between the anthocodia and anthostele, although sometimes interrupted by reducing spicules in the neck zone, and the anthostele is more or less contractile, and thus functional as an operculum of the polyp itself.

In the more evolved species such as *B. sibogae* (= *B. macrospina* Thomson & Dean) and *B. macrospina* (= *Nidalia macrospina* Kükenthal), the cortical spiculation is more massive and rigid, with greater stoutness of spicules. The polyps (more properly the anthocodiae), on the other hand, shorten the stalk, reduce the spicular armature in the introversible neck zone, and become heavier than the anthocodial armature.

Consequently, the discontinuity between the anthocodia and the anthostelar region in spiculation may become more pronounced and a thick-walled, non-contractile calyx as a tubular upgrowth from the cortical coenenchyme (or rind) results. The calycinal spiculation is not arranged interseptally and the apical orifice cannot be completely closed. Here the anthocodia itself, protected by spicular armature, takes a part as an operculum, as is usual in most siphonogorgiids and gorgonaceans. For further details on the evolutionary trend within the genus *Bellonella*, see Utinomi (1957).

In the genus *Siphonogorgia* the arrangement of anthocodial armature is variable between species, as pointed out by Chalmers (1929) in discussing the evolution of species within the genus. It is also probable that this arrangement is intimately concerned with the retractility of the anthocodiae.

As regards the origin of *Siphonogorgia*, in establishing the genus, Kölliker (1875) regarded it as intermediate between the Alcyonacea and the Gorgonacea in modern

systems of classification. Since then, following him, most later authors generally consider that *Siphonogorgia* and allies are derived from the Nephtheidae or at least more related to it than to any other families, a conclusion from which I must most emphatically dissent. The generally accepted ideas, in particular Kükenthal's, that may have been derived from considering its Nephtheid-like mode of growth, associated with the heavier coenenchymal spiculation, and its warm-water distribution restricted to the Indo-Pacific, also appear to be untenable.

The growth form of the colony is, I believe, of limited significance in assessing whether a particular form is primitive or advanced, but reflects general trends in the group. This may reflect the effects of the external environment, especially of water movements, sea temperature and kind of substratum, although there are certain basic characteristics which are apparently never modified by the environment. Thus, such a slight sign of branching in *Nidalia occidentalis* as reported by Gray, as well as a few indistinctly-lobed examples in some species of *Cactogorgia*, suggests a probable evolutionary trend towards ramified siphonogorgiids.

In most of the genera within the family Nephtheidae, the polyps, distributed scatteredly or in groups on branches, are ordinarily not retractile, forming prominent calyces without clear division between the anthocodia and anthostele, and consequently calycinal spicules are completely continuous with those of the cortical coenenchyme of branches and stems. Each polyp is either cylindrical or clavate in shape. In the latter the spicules in the anthocodial region are somewhat bilaterally symmetrical in arrangement, instead of being radial as in most alcyoniids.

The retractile polyps in *Gersemia* and *Paralemnalia*, as in a few exceptional cases, are in all probability a secondary outcome due to the weak development of spiculation in the neck zone. Similar trends as discussed above may probably be observed also within the Gorgonacea.

As regards another aberrant family called Viguieriotidae Bayer (1954*b*), better known as Fascicullariidae Viguier, I have no personal knowledge at present. But it is likely that this family may be a complex of allied forms, having in common only a densely spiculose stalk (" cup " or " involucre ") into which retract numerous polyp-bearing lobes or branches. In other respects they are not related to one another, since one *Viguieriotes* (= *Fascicularia* Viguier) (the simplest) is closely related to the Clavulariidae, one (*Paralcyonium*) to *Bellonella* or *Nidalia*, whereas the remaining one (*Studeriotes*) is more specialized with *Nephthea*-like ramified twigs and polyp armature. Even if these genera may seem to have originated in different ways, there are insufficient reasons for refusing to combine them into a special family.

In conclusion, it need only be mentioned that the retractibility of polyps is indeed one of the important characteristics originally bestowed on the Octocorallia and even all anthozoans. It is a pity that most octocorallian specialists did not lay enough stress on this peculiar character in recognition of various groups within the Octocorallia and their evolutionary trends.

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